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EMBRYOLOGICAL STUDIES

ON

HEXAPODOUS INSECTS.

BY

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EMBRYOLOGICAL STUDIES

ON

HEXAPODOUS INSECTS.

I. DEVELOPMENT OF NEMATUS VENTRICOSUS. (PLATE 1.)

THE only observations on the embryology of the Tenthredinidæ, with which I am acquainted, are those by Prof. A. Winchell,* made in 1863, on *Selandria cerasi* Harris. The eggs of *Nematus ventricosus* are laid along the principal ribs on the under side of the leaf, being simply glued to the surface. They are rather large, .03 long, a little over .01 inch in diameter, regularly cylindrical, the ends being well rounded and white, the chorion being white and transparent. When magnified the egg is seen to be dotted over with pores, appearing like the mouths of little canaliculi (Pl. 1, fig. 8). The eggs of the first brood are laid during the last week in May. My observations were made later in the season, on eggs laid for a second (or possibly a third) brood. The females continued to oviposit from the middle of July, until early in August. The yolk granules vary as usual in size. In the earliest stage observed (July 24) the blastodermic cells had just formed, surrounding the yolk, and crowded three deep at one end of the egg (fig. 1), and at the opposite end forming but a single row (fig. 1*a*). They were of the usual appearance, with a small dark nucleus. The cells, after the amnion has separated from the yolk and forms a true membrane, are much more crowded than usual at the anterior end of the egg, where they actually touch each other; otherwise the amnion does not differ from that of other insects, so far as observed, and remains as an independent membrane, not taking any part in building up the body of the embryo. The mode of formation of the visceral membrane (faltenblatt) was not observed, but just before the embryo leaves the egg, the body and limbs are seen to be surrounded by this membrane, as we shall see farther on.

The next stage observed (fig. 2) may be compared with Bütschli's figure 16 of the embryo of the honey bee,† and between the embryos of the two insects at this stage there is no apparent difference.

* Proceedings Boston Soc. Nat. Hist., ix, p. 321, 1865.

† O. Bütschli. Zur Entwicklungsgeschichte der Biene. Siebold und Kölliker's Zeitschrift. Bd. 21, Heft 4, 1870, p. 519, plates xxiv-xxvii.

The protozonites are now formed, and also the rudiments of the appendages of the head and thorax. The procephalic lobes (the clypeus not being yet differentiated) nearly touch the end of the egg, and are large and full, with the yolk filling the upper portion; the antennæ and mouth-parts are tubercles equal in size, and only differ from the rudiments of the legs in being a little shorter, the second maxillæ, however, being longer than the others and of the same size as the legs; the abdominal legs are as well developed as the thoracic. As in the bee-embryo, the abdomen is not turned over the back, the end being opposite the end of the egg.

A more advanced stage (fig. 3, 3*a*) may be compared with Bütschli's fig. 31*a*, 31*b*, of the honey bee. The rudiments of the antennæ are now much smaller than those of the appendages of the mouth, and the clypeus overlaps the ends of the mandibles, which are now larger than the maxillæ. The first pair of maxillæ are trilobed. The 2d maxillæ are much smaller than the first pair.

The abdomen, when the embryo is a little farther advanced (fig. 4, observed Aug. 2), begins to bend under the body, the end impinging against the end of the egg. The alimentary canal is now formed, the œsophagus can be distinguished, and still more clearly the termination of the intestine (fig. 4,*i*). The labrum (*lb*) is now differentiated from the clypeus (c) and the antennæ are small tubercles, corresponding in their diminished size and retarded development, to the same organs in the bee-embryo, and I am not sure but that this diminutive size of the antennæ, together with its peculiar cubical form, as compared with the rudiments of the mouth-parts, may be the readiest mark by which to identify a hymenopterous embryo, as otherwise it would be difficult to distinguish it from the early stages of a dipterous embryo.

Fig. 5 represents the embryo a day older, when the abdomen is bent under the body so that the tip is opposite the base. The thoracic legs are now large and much longer than the abdominal ones, and are extended backwards. The antennæ seen in profile are squarish.

When the embryo is one day older (fig. 6, 6*a*, 6*b*, 6*c*), the abdomen reaches nearly to the base of the fore legs; it is distinctly bilobed and bears the two finger-shaped tubercles on the upper lobe, which form afterwards two short spine-like hairs. The eyes now appear as a round, dark spot in the centre of an orbicular piece, whose diameter is twice the length of the conical antennæ, which are now divided obscurely into three joints. The powerful muscle (*m*) attached to the mandibles is very distinct, and the œsophagus (*o*) is clearly seen, suddenly dilating into the proventriculus (*p*). The labium (fig. 6*b*, iv) now forms a single plate, from the base of which arise the two palpi. The six joints of the legs (fig. 6*d*) are now indicated, and the yolk mass extends to the middle of the abdomen.

When the embryo is two or three days older (fig. 7), and one day previous to hatching, the dorsal vessel is seen distinctly pulsating, and the body and limbs of the embryo, are enveloped by a delicate membrane (faltenblatt)

which still surrounds the larva for a short period after leaving the egg. The clypeus is now seen to be divided into two portions, while the labrum is elongated. The antennæ still retain their diminutive size and rounded conical shape, being situated just in front of the eyes, while the mandibles are chitinous, triangular in form, and end in four unequal teeth. The first maxillæ are bilobed at the end (seen in profile), and divided longitudinally into two divisions, while the second maxillæ are about half as large. The claws are formed and the body is covered with short spine-like hairs.

The development of this, and probably all of the Tenthredinidæ, accords in its main features with that of the honey bee, the differences in the later stages of the embryo being those which distinguish the caterpillar-like form of the saw-fly larvæ from the footless maggots of the bees, and hence are of secondary importance.

II. DEVELOPMENT OF PULEX CANIS. (PLATE 2.)

The development of *Pulex canis** has been partially investigated by Weismann in his celebrated work "Die Entwicklung der Dipteren." He complains that "though the chorion is not completely opaque, yet he could not observe the more delicate relations, whose investigation alone rewards a connected series of observations, and every attempt to remove it without injuring the yolk-skin (dotterhaut), proved unsuccessful." He describes but one stage in the development, that represented by our fig. 5, and remarks that "at the first glance the great similarity with the embryo of the Tipulidæ is apparent. In this case the primitive band must arise through an actual splitting of the blastoderm (Keimhaut)," and it will be seen from our observations, that this must be the fact. He also remarks, and our observations confirm his statements; "while also the form and position of the primitive band wholly correspond to their relations in Chironomus, so also the composition of each segment is wholly analogous. * * * * The number of primitive segments agrees with that of the Tipulidæ, and the last (twelfth) segment is clearly seen to be due to the union of two pieces pressed together, one dorsal and the other ventral, between which a fine, pointed prolongation of the yolk projects, just as is the case in the same stage of Chironomus (Comp. Taf. iii, fig. 32). The similar formation of the abdomen, indicates a similar origin of the anal opening and rectum (hinterdarmspalte), and so we are led to adopt the existence of a faltenblatt, which in Chironomus is concerned in the formation of these parts. But these observations are not such as to afford proof of such a fact, and we need only state that the embryonal development of the flea comes nearest to that of the Tipulidæ, that the two families belong to those insects which are developed out of a primitive band, which owes its origin to a splitting of the blastoderm." (p. 89, 90.)

*Our eggs were taken from the cat. As several authors regard *P. canis* Bouché and *P. felis* Bouché as the same species, I adopt the name *P. canis* in this paper.

The eggs of the species of Pulex we observed, are short, cylindrical, white, the chorion thin, but the yolk unusually dense, owing to the small size of the granules. The eggs were .02 inch long, and .01¼ inch in diameter.

Though I did not observe the female in the act of oviposition yet I have little doubt that the eggs when first observed, had been deposited only one or two hours. At this time (plate 2, fig. 1) there was observed a vacant space between the yolk and the chorion at the posterior pole, the egg-contents completely filling out the opposite end. Also at this time the end of the egg distinctly bulges out, and in this shallow sinus are four distinct polar cells apparently immersed in protoplasm, and a small indistinct one in addition; they are distinctly nucleated, just as in Chironomus. There seems to be a membrane (I suppose the yolk skin) retaining these polar cells in place. The yolk (*y*) is surrounded by a thin layer of protoplasm two or three times the diameter of the polar cells in thickness; this is the primitive blastodermic skin (*Keimhautblastem* of Weismann) or as it might be termed, *protoblastoderm*.

The egg at this stage may be compared with Weismann's fig. 1, of Chironomus.

About two hours after the stage indicated by fig. 1, the vacant space in the posterior pole of the egg has disappeared, and the yolk and protoblastoderm have pushed up against the yolk skin and polar cells (fig. 2). In half an hour's time more the yolk mass had advanced half way to the polar cells. At this time there were no signs of blastodermic cells.

A few hours after, probably not over thirty after the egg had been laid, the blastoderm cells had appeared, forming a layer around the yolk (fig. 3). This stage may be compared with Weismann's fig. 3. Soon after this the polar cells break down and disappear.

The next stage observed (fig. 4) may be compared with Weismann's fig. 18. The amnion (*am*) is as usual, lying next to the chorion; while the faltenblatt (*fb*) may be traced enveloping closely the primitive band. The cephalic lobes and succeeding protozonites are formed. A slight interval separates the end of the future abdomen from the procephalic lobes. The egg at this stage is about forty-eight hours old. Fig. 4*a* represents the eggs seen at the same period from above, the extremity of the abdomen resting on the upper surface of the posterior two-thirds of the yolk, and the procephalic lobes and two succeeding protozonites resting upon the anterior end of the yolk. The median furrow is indicated at the posterior end of the egg; the abdominal portion of the primitive band in view is seen to be narrower at the end than at the base, and ending abruptly.

A little more advanced stage observed in the same egg when it has been laid seventy-two hours, is represented at figs. 4*b* and 4*c*. The outer yolk layer (*oy*) is very distinct, and seems to be composed of partially formed muscular tissue and broken down yolk cells, while the inner layer (*iy*) or central portion, is as usual darker than the rest of the egg. The faltenblatt,

or visceral membrane, may now be distinctly seen passing from the procephalic lobes to the last abdominal protozonite, showing that it is as complete an envelope to the embryo as the amnion. The antennæ (I), mandibles, and two pairs of maxillæ are beginning to bud out, and the clypeus (C) is differentiated from the procephalic lobes, forming a simple fold of the membrane.

Shortly after (I did not observe the number of hours, but probably in less than twenty-four) the embryo appears as in fig. 5, which may be compared to Weismann's fig. 30. The inner yolk mass is now much smaller than before, being confined to an oval mass. The rudiments of the appendages of the head have increased in length; and there are plainly indicated ten abdominal segments, but the tenth appears to be afterwards folded in to form the end of the body, as in Chironomus, according to Weismann's observations. Fig. 5*a* represents a little later stage, the same as figured by Weismann (Tab. vii, fig. 62).

At a still later stage (fig. 6, 6*a*) the head is walled in; the second pair of maxillæ have approximated; the mandibles touch each other on their future cutting edges, over which the labrum laps, while the first maxillæ are still remote from each other. The dorsal part of the embryo has now closed in, and the next stage is the folding of the end of the abdomen under the body. This occurs when the egg has been laid four days. The process is just as has been described and figured by Weismann in Chironomus. Fig. 7 gives an idea of the appearance of the embryo when the act is half accomplished, the ninth and terminal segment of the body pressing against the end of the egg. The next day the body has extended twice its former length, and the embryo is doubled upon itself so that the end of the body rests under the head. At this time the faltenblatt loosely envelops the embryo. The supposed egg-opener is distinct, and shortly before hatching the embryo appears just like the freshly hatched larva. It leaves the egg in about six days after the egg is laid.

We have seen that in its embryology Pulex does not differ from that of Chironomus, with whose development that of Simulium essentially agrees; and though we know nothing of the embryology of the Mycetophilidæ, yet when we come to compare the larvæ of Pulex with those of the Mycetophilidæ, there is a general resemblance, which does not militate against the view of Haliday, who first suggested that the Pulicidæ are related to this dipterous family.

III. DEVELOPMENT OF ATTELABUS RHOIS. (PLATE 3, FIGS. 1–5.)

The eggs of this species of Attelabus are readily obtained by opening the singular thimble-like rolls, made by the female late in June and during the month of July, on the alder. When about to oviposit, the female picks up a leaf with her mandibles, and begins to eat a slit near the base of the leaf, on each side of the midrib and at right angles to it, so that the leaf may be folded

together. Before beginning to roll up the leaf she gnaws the stem nearly off, so that after the roll is made, and has dried for perhaps a day, it is easily detached by the wind and falls to the ground. Then folding the leaf, she tightly rolls it up, neatly tucking in the ends, until a compact, cylindrical, solid mass is formed. Before the leaf is entirely rolled, she deposits a single egg, rarely two, in the middle, next to the midrib, in a little cavity, where it lies loose. While she is thus engaged the male may often be seen standing at the other end of the leaf, or on an adjoining one. I once saw a female pick up a leaf with her jaws, then stop, and run back to receive the embraces of the male, and then resume her work. In another case I saw the sexes unite after a roll had been half made, so that it is probable that union occurs several times at short intervals, as I have observed to be the case with *Gastrophysa polygoni*. These rolls remain on the bushes sometimes for several days, but probably drop by the time the larva escapes from the egg, and it seems probable that the larva at once eats the inside of the roll, which thus answers to the leaf bud or seed in which other larvæ of this family live.

The only coleopterous insect whose development in the egg is known,* is Donacia, whose embryology was first described by Kölliker† and more fully by Melnikow‡ in 1869. It will be seen that the embryology of Attelabus essentially agrees with that of Donacia, a member of a remotely allied family. The eggs of *Attelabus rhois* are nearly spherical, though a little longer than thick, .04 inch long, and .03 in diameter. The chorion is thin, smooth, very transparent; the yolk is made up of pale green, fine granules.

When the egg has been laid about (probably less than) twenty-four hours, I could detect the blastodermic cells in course of formation (plate 3, fig. 1), though the earliest appearance of the nucleus at the periphery of the yolk (see Melnikow's fig. 1) was not seen. But the stage at which I observed them may be compared with his fig. 2. The outer row of blastodermic cells had been formed, but in the inner row the molecules of the yolk mass were arranging themselves around the nucleus, and the cell walls were partially formed, being evidently as first shown by Weismann§ filled with yolk molecules.

When the egg is fully twenty-four hours old, the blastoderm, entirely surrounding the yolk, is fully formed, as easily seen on crushing the egg, and the primitive band is confined to one side of the egg. The cells of the blastoderm (fig. 2) are pressed side by side, being a little elongated, and the dark nucleus is much more distinct than before, while the yolk is distinctly separated from the yolk.

Fig. 3 represents the egg after it has been laid about thirty-six hours, and

*Joly (Ann. des Sc. Nat., 3d Ser., Tom. 2, 1844, p. 5) has given a brief account of the embryology of *Colaspis atra*, but only figures the later stages just before the embryo leaves the egg. His observations are not sufficient to enable us to decide whether Colaspis is developed like other Chrysomelids or not.

†Observationes de prima Insectorum Genesi, etc. Turici, 1842.

‡ Beiträge zur Embryonalentwickelung der Insekten, Archiv für Naturgeschichte, vol. 35, p. 136. 1869.

§ Die Entwicklung der Dipteren. See Tab. iv, fig. 52, 53, 53A, 53B, E.

may at this time be compared with the stage in Donacia, represented by Melnikow's fig. 5. The primitive band rests entirely on the outside of the yolk, the thickened portion, or so-called primitive band, covering two-thirds of its surface. At the anterior pole of the egg it is a little depressed. The stages indicated by Melnikow's figs. 6–11, were not observed, but the next step in the development of Attelabus, is the extension of the primitive band, the ends meeting so as entirely to surround the yolk. At this time the median furrow in the band is distinct, with the appendages just beginning to bud out. Though the faltenblatt could be seen passing around the cephalic appendages, I could not make out its relations so clearly as shown in Melnikow's fig. 12, with which this stage may be compared.

In the succeeding stage observed (fig. 4) the procephalic lobes, clypeus, and appendages of the head and thorax, are well developed. The rudiments of the mandibles are rather larger than the other mouth-parts. The four protozonites of the head may be distinctly seen, the procephalic lobes forming the first. The germ still floats upon the yolk, which fills the inner half of the primitive band. The yolk granules are contained in polygonal vesicles just as in Donacia. The end of the abdomen, consisting of eleven protozonites, has retreated from the procephalic lobes, allowing a portion of the yolk to impinge against the chorion.

Fig. 5 represents the embryo a day older. The mouth-parts are a little longer, and the articulations in the legs (fig. *5a*) are distinct. The cells of the amnion are very distinct, but scattered and irregular, and the faltenblatt is seen enveloping the body and limbs, being composed of scattered cells like those of the amnion. This stage may be compared with Melnikow's fig. 13.

In its essential features the embryology of Attelabus is similar to that of Donacia, the primitive band resting on the outside of the yolk, being an "ectoblast," to use Dr. A. Dohrn's expression. It is after the stages above described that the embryo assumes the form peculiar to its genus and family. The larvæ began to hatch out about the middle of July. I did not ascertain the exact number of days from the time of oviposition to the exclusion of the embryo, but judge that it required about a week.

IV. DEVELOPMENT OF TELEPHORUS FRAXINI. (PLATE 3, FIGS. 6–8.)

The development of this beetle in its earliest stages, is of remarkable interest, since it differs from the other Coleoptera whose development is known, in the primitive band floating in the centre of the yolk, instead of surrounding it.

On the 26th of June, a female which I had put in confinement hoping to obtain some eggs from it, laid a few loose in the bottom of the vial. They were broad, ovate, pale yellowish in color, with a thin, smooth, transparent chorion. The yolk cells varied in size, from that of the molecules which had collected around the periphery, to a few large granules situated in the

centre of the yolk and about one-sixth the diameter of the egg. On the 30th of June several of the eggs were observed with the primitive band (plate 3, fig. 6) forming a broad, sigmoid, yellowish streak. The anterior end was the broader, and dilated slightly at the end, forming the procephalic lobes, and consisting of fine yolk granules, becoming finer posteriorly, until its structure could not be determined, as it had sunk in towards the centre of the yolk. The protozonites had not yet been indicated. At this stage the appearance presented by the germ was almost identical with that of the eggs of Lecanium, observed by myself, several years previously, and of *Aspidiotus nerii*, which has been figured by Metznikow* (pl. xxxii, figs. 7–10, and also his figure of the embryo of Aphis rosæ). It is also similar to the eggs at this stage of Calopteryx and Agrion, as figured by Brandt, † and of the Pediculina described and figured by Melnikow.

In the next stage observed, the embryo rested on the outside of the yolk and in no wise differed from the same stage in Attelabus (see fig. 4), the rudiments of the head and the protozonites, and the disposition of the body on the yolk being the same. The two membranes, the amnion and faltenblatt, are also the same.

When the embryo is about eight days old (fig. 7, ventral view), and nearly ready to hatch, the clypeus is fully differentiated, and the mouth-parts are as in Attelabus, the yolk still occupying a large portion of the egg.

Fig. 8 represents the embryo seen ventrally, and ready to escape from the egg; it presents very much the same appearance as the Donacia embryo at a little later stage, figured by Kölliker‡ (Tab. iii, fig. vi), the differences being only such as we would expect to find in embryos belonging to two widely different families. The abdomen is bent under the body so that the tip reaches nearly to the end of the labium. The yolk mass is restricted to a small portion of the body. The antennæ are still embryonic, being simple tubercles, but the mandibles meet beneath the labium. The second maxillæ have united to form the labium, and the head is distinct from the thorax.

By the 6th of July all the embryos had hatched, the period required for the growth and hatching of the embryo being about ten days.

V. DEVELOPMENT OF CHRYSOMELA (GASTROPHYSA) POLYGONI (PLATE 3, FIG. 9) AND MYSIA 13-PUNCTATA.

Our observations are very fragmentary, and they are given only to show that the development of these two Chrysomelidans agrees substantially with that of Donacia.

The eggs of *Gastrophysa polygoni* are long, cylindrical, yellow, and laid in patches on the under side of the leaves of different plants. The chorion

* Siebold und Kölliker's Zeitschrift, 1866, p. 389.

† Beiträge zur Entwicklungsgeschichte der Libelluliden und Hemipteren. Mém. Acad. Imp. des Sciences. St. Petersbourg, 1869.

‡ Observationes de prima Insectorum Genesi. Turici, 1842.

is smooth and transparent. Two days after the eggs were laid the embryo had arrived at the stage indicated by pl. 3, fig. 9, which may be compared with Melnikow's fig. 14 of the embryo of Donacia. It also bears a striking resemblance to the embryo (in the same stage of growth) of Chironomus, as figured by Weismann (Tab. ii, fig. 21, 22), and I think it would be impossible for an experienced embryologist to tell whether the germ at this stage was destined to become a dipterous or coleopterous insect. On account of the large clypeus filled with yolk granules, as in Chironomus, and the relation of the rudiments of the cephalic appendages and also of the faltenblatt (which compare with Weismann's fig. 20), one would think it resembled a dipter the more. I did not observe the earlier stages so as to ascertain whether the primitive band is at first endo or ectoblastic.

The eggs of *Mysia 13-punctata*, one of the Coccinellidæ, are oval cylindrical, not so long as those of Chrysomela, and are yellow, with a thin, smooth chorion. They were laid in confinement on the 16th of July, and two days after, a slight examination sufficed to show that the primitive band in this genus rests on the outside of the yolk, the egg at this stage appearing much as that of Attelabus (fig. 3), though not quite so far advanced.

These fragmentary observations on species of the Coleopterous families, Lampyridæ (Telephorus), Curculionidæ (Attelabus), Chrysomelidæ (Donacia, by Kölliker and Melnikow, and Gastrophysa) and Coccinellidæ (Mysia), may be taken as tending to show that (with the exception of Telephorus in its earliest condition, when the primitive band floats in the centre of the yolk, as in the Hemiptera and Libellulidæ) the mode of development in the Coleoptera is nearly identical with that of the Diptera and also the Hymenoptera; the formation of the embryonal membranes seems also to be nearly identical.

Newport's observations on the embryology of Stylops * are not detailed enough for us to judge how far the development of this singular Coleopter agrees or disagrees with that of the group generally, except that he states that the primitive band rests on the outside of the yolk.

VI. DEVELOPMENT OF CHRYSOPA OCULATA. (PLATE 3, FIGS. 10–13.)

The first observations on the embryology of the family of Hemerobidæ, of which Chrysopa is a member, were made by Dr. H. Hagen,† on *Osmylus maculatus* Fabr. He describes the three membranes surrounding the embryo, *i. e.* an outer covering forming a network of polygonal pits around the chorion ("Umhüllungshaut"), the chorion and the "dotterhaut," or amnion. "The development of the primitive band begins on the fourth day, the ventral side presenting outwards, first at the head and a little later in the posterior abdominal segments." From this I suppose that the primitive band does

* The Natural History, Anatomy, and Development of Meloe. Linnæan Trans. xx, Tab. 14, 1847.

† Die Entwicklung und der innere Bau von Osmylus. (Published in the "Linnæa Entomologica," Stettin, 1852.)

not float at first in the centre of the egg, but from the first rests on the outside of the yolk. On the seventh day it presents the appearance indicated by my fig. 11, of Chrysopa. On the tenth day the germ is developed much as in my fig. 12; and the embryo hatches on the twelfth.

F. Brauer* has studied the later developmental history of *Mantispa pagana* Fabr. He states that the "turning of the embryo begins on the eighth day, and on the ninth is completed." After this the position of the body and its appendages is essentially like that of Chrysopa, the differences being due to the greater length of the body of Mantispa. The eggs are stalked as in Chrysopa, and the large micropyle is similar to that of the eggs of Chrysopa. He notices the chorion and the amnion ("dotterhaut"). At the expiration of twenty-one days after oviposition the embryo escapes from the egg.

The female of *Chrysopa oculata* Say, the species upon which the following observations were made, laid between forty and fifty eggs (one in confinement laid forty-six eggs; another eighteen eggs, or egg stalks, but her reproductive powers were evidently impaired, or else she had laid some eggs before capture, as there were only nine well developed eggs in the batch, and nine stalks, some only half the usual height, others with the knob of cement at the end to which the egg is ordinarily fastened). The eggs (.04 inch long, .02 in diameter) are at first pale green, turning grayish just before the embryo is hatched. The eggs are evidently stuck on to the end of the pedial after the latter has been formed, as in one case an egg was glued to the stalk very much out of centre, the insect's ovipositor not having aimed straight, so to speak, at the mass of cement. The chorion is not very transparent, though smooth. The micropyle, like that of Corixa, forms a conspicuous button-like knob, resembling the finely milled head of a screw. The yolk granules are remarkably small, so that the primitive band is in strong contrast to the yolk in color and density. When the egg is crushed, the yolk does not flow out as a liquid, bearing globules along the stream, but in a pasty mass, somewhat, but not so marked as in the eggs of Limulus when similarly treated, and I would question whether the fineness of the yolk granules, and the denseness of the yolk be not connected in the way of cause and effect, with the exposed situation of the eggs of Chrysopa.

The eggs were laid in confinement on the 3d of July, and I did not succeed in watching the formation of the amnion, or seeing the earlier steps in the formation of the primitive band, owing to the opacity of the chorion and the density of the yolk. Pl. 3, fig. 10, 10*a*, 10*b*, indicates the embryo when three days old, the eggs being observed July 6th. At this time the amnion was a closed sac entirely surrounding the yolk; the cells were unusually round and distinct, with a well defined nucleus, and were less crowded than usual, and they may be viewed when looking at the egg as an opaque object, appearing as greenish opaque dots, probably reflecting the

* Beitrage zur Kenntniss des inneren Baues und der Verwandlung der Neuropteren. Verhandlungen des Zool.-Bot. Vereins in Wien. Bd. v, p. 701. 1855.

green tint of the yolk. The cells are crowded thickly at each end of the egg, being seen more readily when the yolk thins out.

The primitive band is fully formed, the protozonites being distinctly marked, the transverse impressed lines indicating the primitive segments being distinct, and the median furrow easily discerned. The procephalic lobes are well formed, being regularly convex in front, broader than the rest of the band. The abdominal portion of the band is a little more than half as wide as the anterior portion. The end of the band seen on the dorsal side of the egg forms a distinct region of the band which may be called the primitive postabdomen; it forms a rounded portion separated by a suture from the rest of the abdomen, beyond which suture the median furrow does not pass.

There are no indications of limbs. The germ lies on the outside of the yolk, the ventral side facing outwards, the end of the abdomen curving around the yolk and resting on the dorsal surface of the egg, as seen in fig. 9*b*. In profile (fig. 10) the under or dorsal side of the germ sinks into the yolk as in all insects, but the line between the band and the yolk mass is remarkably distinct; the under side of each protozonite is convex, especially in those segments nearest the procephalic lobes, and these latter are broad, orbicular, seen in profile. The primitive band is pale yellow, growing paler towards the edges; and in this respect, though perhaps unimportant, the germ differs remarkably from that of any other insects with which I am acquainted, and also the eggs of any Crustacean or Arachnidan referred to by authors or noticed by myself. Hagen describes colored spots in the primitive band of Osmylus, like those noticed farther on in the present insect, so that this high color of the primitive band may be a characteristic of the Hemerobidæ (in the broad sense, including the Ascalaphi and Mantispæ). This stage may be compared also with that of Chironomus, represented by Weismann's pl. ii, fig. 18, the differences apparently being due to the greater density in the yolk and primitive band of Chrysopa, rather than to any morphological differences. It also more closely agrees with the stage of Corixa indicated by Melnikow's fig. 15.

Figure 11 represents an egg older than the other, and somewhat flattened by pressure, the primitive band being distorted; the sutures are, however, clearly indicated. At this time the procephalic lobes are pale yellow, while the rest of the primitive band is greenish yellow, and the postabdomen is brownish, and there are brownish spots at most of the sutures.

In another egg which had been laid between three and four days (laid July 4–5th, and studied July 7th), the appendages had appeared (fig. 12). While the amnion is distinct, the faltenblatt is also distinctly seen closely surrounding the head and the end of that part of the abdomen in sight, the end being still folded on the back of the yolk, so that there is no doubt but that the whole body is enveloped by it, as in the Coleoptera. Owing to the opacity of the yolk, I could not trace it along the side of the cephalic and thoracic portion of the band. How far its relations to the yolk mass, at the

period of turning of the embryo, is like that described by Brandt in his memoir on the development of Calopteryx and Agrion, I could not determine.

The rudiments of the clypeus now appear as a tubercle arising from between the procephalic lobes, which hang over the area destined to form the mouth. The antennæ (I) are plainly seen to depend from near the edge of the lobes. The three succeeding pairs of appendages (II–IV, the mandibles, and 1st and 2d maxillæ) are alike in size and appearance, while the three pairs of legs are directed obliquely backwards and meet on the median line of the band. The germ is now more highly colored than before, being quite bright yellow, while at the base of the abdominal portion of the band are two large, rounded, brown spots, which meet on the median furrow, and this band is spotted with brown posteriorly, as seen in fig. 10.

At this time the germ is very similar to the germs of Diplax and Calopteryx, and there is apparently no essential difference, except that the germ of Chrysopa does not sink into the yolk as do those of the Libellulidæ.

I am inclined not to regard this as of much importance, as even in the Hemiptera as shown by Metznikow and Brandt, the primitive band varies in degree of immersion in the yolk, being most marked in Aspidiotus and least so in Corixa, the primitive band in the latter being surrounded by the yolk only at the earliest moments of its formation (see Metznikow's fig. 7, in which the band is only half as long as the egg), and it is not improbable that the primitive band in Chrysopa is at first surrounded by the yolk, while in Chironomus (fig. 18 of Weismann), the germ sinks partially down into the yolk. (See Metznikow's fig. 15 of Corixa, with which the present stage may be compared.) We are also strikingly reminded of the primitive band of the Araneina, as it is seen floating on the surface of the yolk, with the rudiments of the mouth-parts and limbs projecting outwards as tubercles (compare Claparède's fig. 33*).

Of course the limbs did not appear at once in this stage, as seen in this egg; their rudiments must have appeared synchronously with the segments seen in the preceding stage, though they could not be detected, owing to the difficulty of examining the eggs from the opacity of the chorion. The next steps in the growth of the embryo were not observed, including the bending of the abdomen beneath the body. The embryo, however, does not turn around in its shell, as will be seen by looking at fig. 13 (which rudely and very imperfectly represents the embryo when between five and six days old), where the head remains next to the micropyle, as in the earliest period of its development. The process of turning is not, then, essential in insects, and for this reason I am inclined to think that as in the Coleoptera, the faltenblatt is not drawn in to form a yolk bag as described by Brandt in the Libellulidæ.

The embryo is hatched in six or seven days from the time of oviposition, just about half the time occupied in the development of Osmylus, as stated by Dr. Hagen, and one-third the time occupied by *Mantispa pagana*.

* Recherches sur l'Evolution des Araignées. Utrecht, 1862.

While, as we have seen, Chrysopa in its earliest stages, *i. e.* in the mode of formation of the primitive band, probably agrees closely with Corixa, it afterwards, at the time when the limbs bud out, agrees more closely with the Libellulidæ, the difference being that the germ of the Libellulidæ floats within the yolk, while that of Chrysopa (like that of Corixa) rests upon the outside of the yolk. This difference of position of the germ seems to be of but slight importance, especially when we bear in mind the great diversity in the position of the yolk in the different genera of the Hemiptera, there being every grade from Corixa, in which the germ is immersed only at the first beginning of the primitive band, up to Aspidiotus, where it forms a large distinct S-shaped band. We have also seen that in the Coleoptera the germ of Attelabus is, so far as we were able to find, never immersed in the yolk, while in Telephorus it has the S-shape, characteristic of Aspidiotus.*

The embryology of Chrysopa does not essentially differ, then, from that of the Libellulidæ. We now know that the development of Osmylus, and probably Mantispa is similar to that of Chrysopa, and hence we may suppose that the other members of the family Hemerobidæ are developed in the same manner. The Libellulidæ are considered a group of the Pseudoneuroptera, while the Hemerobidæ are types of the "true" Neuroptera. But having shown that the mode of development of these two families is as similar as in two families of the Hemiptera, we would ask what becomes of the distinction between the "Pseudo" Neuroptera and "true" Neuroptera? Never believing that the differences were quite enough to separate the Linnæan Neuroptera into two independent orders or suborders (whichever we may choose to call them), we would now ask if embryology does not give independent testimony as to the close alliance at least of the Libellulidæ and Hemerobidæ, even if we go no farther?

We have shown that the development of Nematus agrees with that of Apis, as studied by Bütschli, while that of the Formicidæ is much the same, as shown by Ganin. The development of the egg-parasites (Proctotrypidæ) is in many respects very extraordinary, and seems obviously connected with the exceptional mode of life of the larva. Of the development of the Lepidoptera we know little beyond Herold's researches. Ganin,† however, states that the development of the Hymenoptera and Lepidoptera, as regards the mode of formation of the amnion, its relation to the embryo, as also the physiological role it plays during embryonic development, is entirely similar in the two groups. He farther says that the amnion is developed in Apis (according to Weismann's investigations) exactly as in the Formicidæ and Lepidoptera, and adds that such is the case in many Ichneumonidæ and

*For the reason that the primitive band varies so much in its position in relation to the yolk, closely allied insects varying greatly in this respect, while in some genera of parasitic Ichneumon flies (Teleas, Polynema, Platygaster, the primitive band is not formed until the second larval stage is reached, according to Ganin), I have been led to think that Dr. Dohrn's classification of insects into entoblasts and endoblasts (see Ent. Zeitung, Stettin., 1870, p. 244) is quite artificial.

† Uber die Embryonalhalle der Hymenopteren und Lepidopteren Embryonen, 1869.

Cynipidæ. He adds farther that the mode of development of the embryonal membranes is the same in all insects with a complete metamorphosis. In all these insects the amnion takes no part in building up the body of the embryo, while in the ametabolous lice they do, and thus, he says, in earlier times this may have been the case with all ametabolous insects.

We have also seen that the Diptera and Coleoptera are apparently developed in much the same manner, and that they agree substantially with the Hymenoptera. The greatest divergence is presented in the Hemiptera and Neuroptera (the Phryganeidæ and Poduridæ are similar in their embryology and resemble that of Attelabus in perhaps the most important features, though with some peculiarities of their own). These differences are not improbably owing (at least this explanation may be better than none at all) to the fact that the larvæ are born with a peculiar form, their metamorphosis being incomplete. Indeed in several of the instances in which the embryology of insects has been studied, we find that the divergences from the normal mode of development are correlated with important biological differences of the larval or adult insect, and I think it will be one of the points to be established in the future, *i. e.*, how far the differences in the embryology of animals are due to differences in the habits and instincts of the larvæ and adults.

Thus embryology will not prove an infallible guide in the classification of animals, but is to be used with the same caution as anatomical and biological characters. So also with the postembryonic changes in insects; the diversity of the mode of metamorphosis in the families of the Neuroptera and Orthoptera for example, is perhaps of less importance in taxonomy than many will allow.

So far as our present investigations have gone, we may conclude that there is a remarkable uniformity in the mode of development of the Hexapoda, as much so perhaps as in the Decapodous Crustacea, and it is difficult to determine what embryological characters may be set down as distinguishing even the different suborders. These characters, whatever they may be, do not probably reside in the embryonal membranes, or in the relation of the primitive band to the yolk. It is more probable that they will be found in the form of the advanced embryos. For example, we now know that the embryos of the Isopod Crustacea only differ from those of the Amphipods while in the egg, by having the end of the abdomen bent over the back, while in the latter (Amphipods) it is curved beneath the body, as pointed out by Fritz Müller. We may find that the cylindrical, more or less caterpillar or maggot-like form of the Hymenopterous, Lepidopterous, and Dipterous larvæ, which I have called* *eruciform*, have a common mode of development, in distinction from the larvæ of the Neuroptera and Orthoptera, which do not have a worm-like body, the head being large, the legs usually like those of the adult, and the body elongated and flattened, or oval, more or less like a mite. This general type I have called *leptiform*, and believe that

*American Naturalist vol. iv, p. 756, v, p. 51, 567, 1871.

it is the primitive form of the paleozoic larvæ, in accordance with Fritz Müller's opinion "that the 'incomplete metamorphosis' of the Orthoptera is the primitive one, *inherited* from the original parents of all insects, and the 'complete metamorphosis' of the Coleoptera, Diptera, etc., is a subsequently acquired one."* It should be noticed in this connection that the maggot-like larvæ of the weevils (Attelabus), which are rather eruciform than leptiform, are developed much like the Diptera, while the somewhat eruciform larvæ of the Phryganeidæ also resemble the Diptera in form. (The Poduridæ form an apparent exception, as they develop like the Phryganeidæ, though decidedly leptiform when hatched.) But such speculations may prove to be premature, our present knowledge of the embryology of the Hexapods being far less perfect than that of the embryonic stages of the Crustacea.

*Für Darwin, Eng. Transl., p. 121.

EXPLANATION OF PLATES.

PLATE 1. NEMATUS VENTRICOSUS.

Figure 1. Anterior and posterior end of egg, showing formation of blastoderm.
Figure 2. Primitive band, with rudiments of appendages of head and thorax. I, antenna; II, mandible; III, maxilla; IV, 2d maxilla. (The lettering is the same in all the plates.)
Figure 3. Ventral view of the embryo a little farther advanced. *3a*, the same enlarged, showing the clypeus (*c*) overhanging the labrum (*lb*); the maxillæ are trilobed.
Figure 4. The body has increased in length, the abdomen beginning to bend down.
Figure 5. The head separate from the thorax, and the abdomen bent beneath the body.
Figure 6. The embryo still farther advanced, the abdominal legs being distinct. *6a*, *6b*, views of the head; *o*, œsophagus; *p*, proventriculus; *m*, muscles attached to the mandibles; *6c*, tubercles on the end of the abdomen, destined to form hairs; *6d*, a leg.
Figure 7. Embryo one day previous to hatching, the end of the abdomen reaching to the anterior feet. *dl*, faltenblatt.

PLATE 2. PULEX CANIS.

Figure 1. End of egg after having been laid one or two hours.
Figure 2. The same, two hours after the stage represented by fig. 1.
Figure 3. Egg showing layer of blastodermic cells.
Figure 4. Blastoderm, with the procephalic lobes and protozonites indicated, also the faltenblatt (*fb*) and amnion lying next to the chorion. *4a*, dorsal view of the same; *4b*, side view of end of the egg, when a little older, showing the head and body enveloped by the faltenblatt (*fb*) and the inner and outer yolk layers; *4c*, the same enlarged; *am*, amnion.
Figure 5. Embryo about three days old; *5a*, a little later stage.
Figure 6. Head completely walled in. Embryo four days old; *6a*, head enlarged.
Figure 7. Embryo about a day before hatching.

PLATE 3. FIGS. 1 TO 5, ATTELABUS RHOIS; FIGS. 6 TO 8, TELEPHORUS FRAXINI; FIG. 9, CHRYSOMELA POLYGONI; FIGS. 10 TO 13, CHRYSOPA OCULATA.

Figure 1. Portion of egg, showing layer of blastoderm cells, (*am*) destined to form the amnion; *y*, half formed primitive band.
Figure 2. The same when the egg has been laid about 24 hours.
Figure 3. Egg, 36 hours after being laid.
Figure 4. Protozonites, and rudimentary appendages of head and thorax.
Figure 5. The embryo a day older; *5a*, legs showing articulations.
Figure 6. Eggs with the S-shaped primitive band floating in the yolk.
Figure 7. The embryo about eight days old.
Figure 8. The embryo just ready to hatch.
Figure 9. Embryo two days old.
Figure 10. Eggs three days after being laid; 10, side view of primitive band; *10a*, ventral view of the band; *10b*, dorsal view of the egg, showing abdominal end of the germ.
Figure 11. Ventral view of germ (the yolk cells are represented three times too large, as the largest only measure 1-4000 of an inch in diameter).
Figure 12. Embryo three or four days old.
Figure 13. Embryo ready to hatch.

[The observations were made with Zentmeyer's 1 1-2 and 4-10 inch objectives.]


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6a
6b
6c
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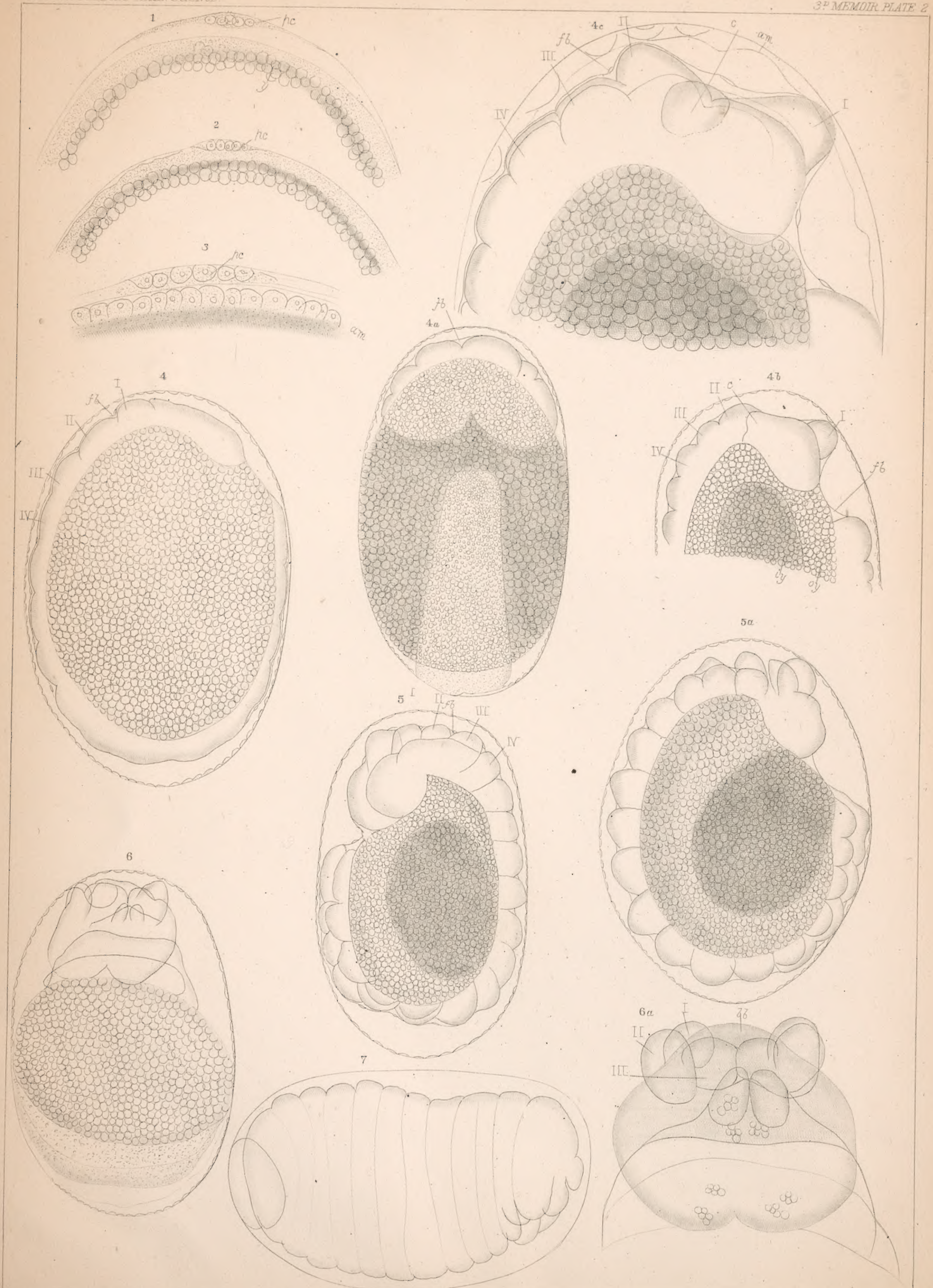

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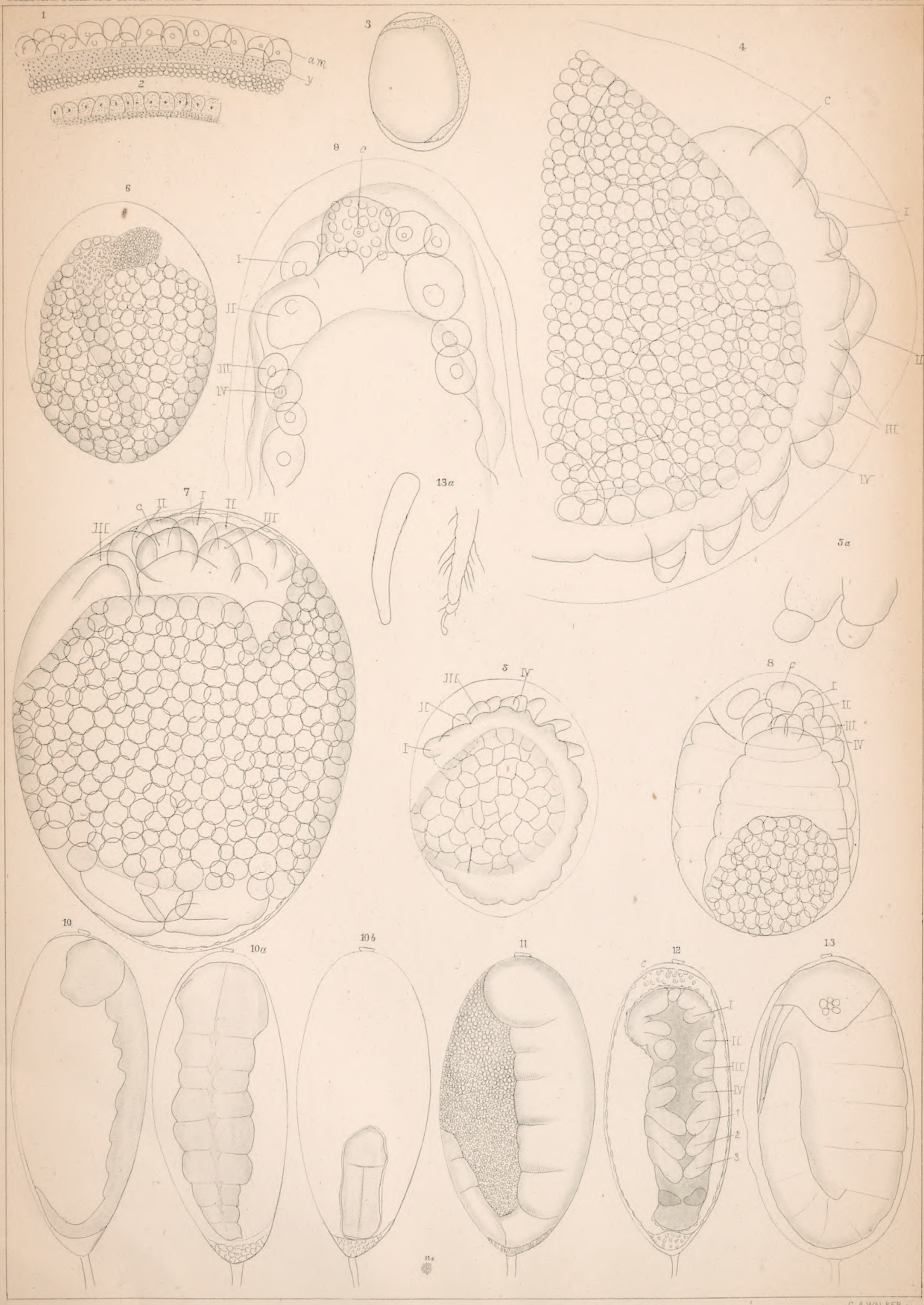

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